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Aspects of the ecology and behaviour of the thick-tailed bushbaby Galago crassicaudatus

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first sniff the fruits and pick only those which were ripe, whereas others picked unripe fruits and then dropped them onto the ground. Even ripe fruits would be dropped accidentally or knocked off by the animal's movements but no interest was shown in the fruit once it had fallen.

Fruits were either picked directly with the mouth or first guided to the mouth with one hand and then carried away to be eaten in comfort (figure 15a). Some of the actions involved in fruit-eating have been illustrated in figure 16 in comparison with G. senegalensis. Small fruits were held in one hand while part of the peel was chewed away and discarded by spitting or flicking the head. The soft insides were then licked or scraped out with the teeth and the remaining shell dropped to the ground. Large fruits were sometimes eaten in a similar way without being picked.

G. crassicaudatus would remain in the vicinity of fruit trees for several hours at a time and return to them frequently during the night, but feeding seldom lasted for more than twenty minutes at a time. When several bushbabies were attracted to a fruit tree at one time they occasionally quarrelled mildly but no serious antagonism was seen.

The use of fruit is probably the most important dietry adaptation of this species. G. crassicaudatus are absent from regions where fruits are not abundant during at least six months of the year and this appears to be a significant factor which limits their distribution.

10.3 The Use of Seeds and Dry Fruits

Seed pods and woody fruits were often found on the ground or lodged in the forks of large trees. Bushbabies came across these items during the normal course of movement or while moving slowly in the dense tangle of vegetation close to the ground. One individual was observed to grab a seed off the ground with its mouth and return to a tree fork before eating it. Usually the food was discovered and consumed while the bushbaby sat on the ground. They searched among the leaves with the hands or nose, picking up seeds with one hand and chewing away the husk noisily. In Rhodesia, foraging on the ground in the open was not uncommon and it sometimes lasted for fifteen minutes at a time. Seeds and dry fruits were most utilized in the winter when other foods were in short supply.

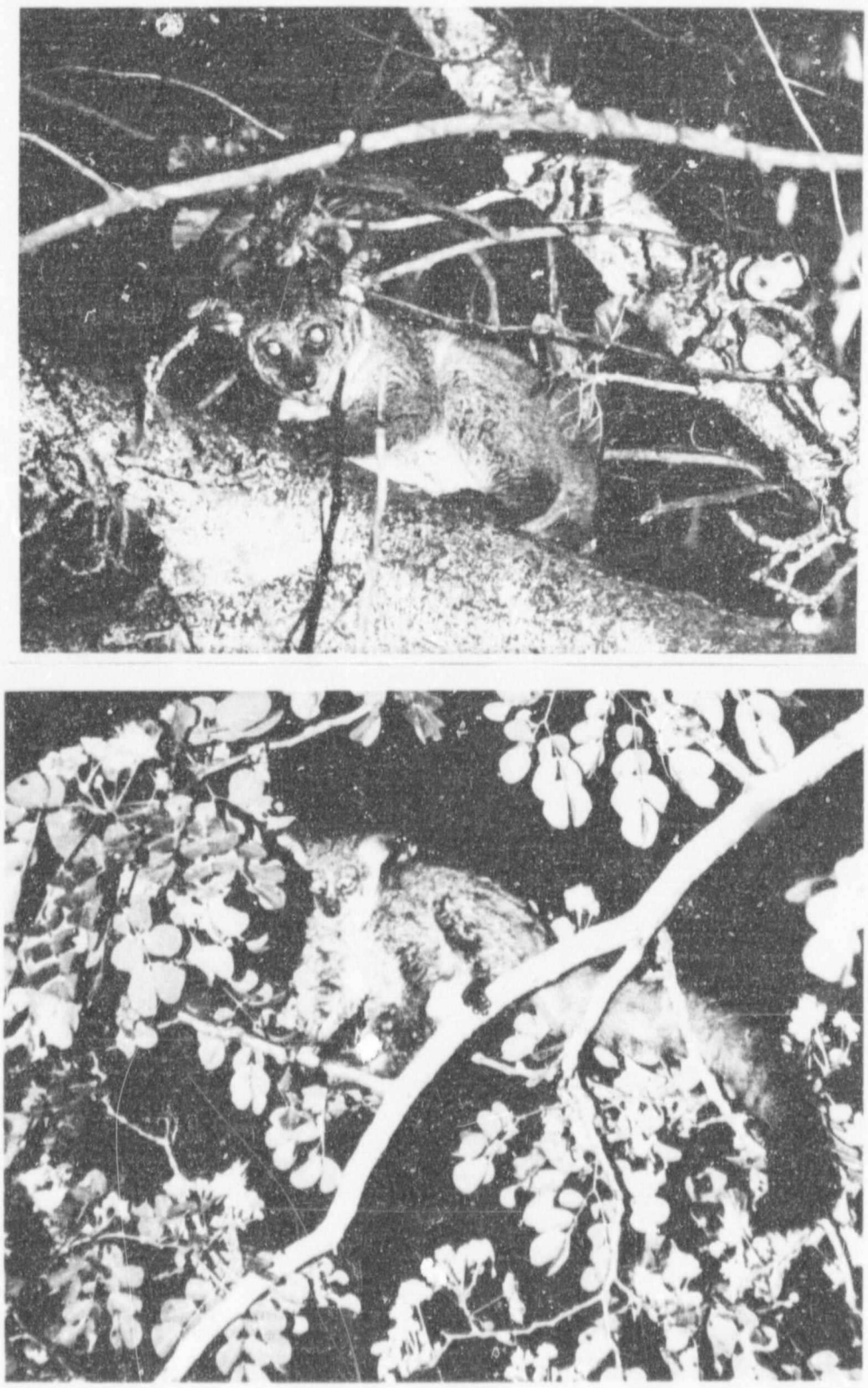


Figure 15. Photographs of G. crassicaudatus taken at night. (a) An adult male feeding on wild figs (Ficus sycamorus). (b) An adult female moving within a flowering Albizia. Note the reflection of flash from the tapetum of the eyes, which in the lower photograph are half-closed. This animal has a dark tip to its tail.

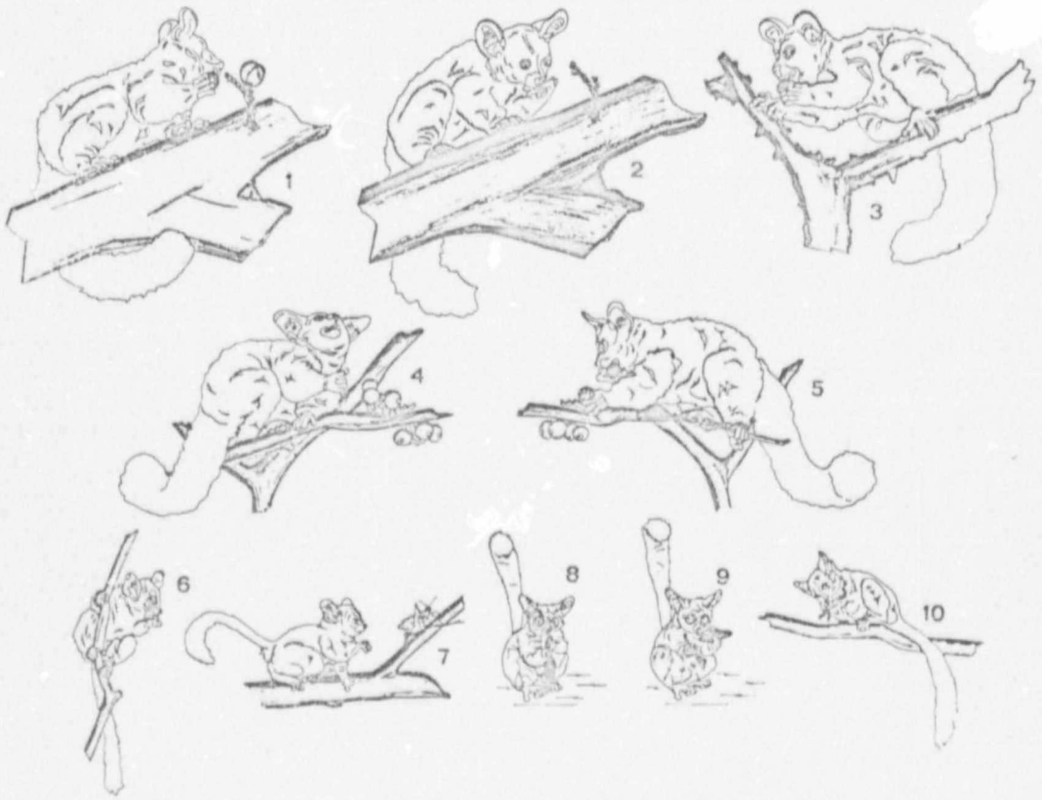


Figure 16. Drawings taken from photographs to show the use of the hands in G. crassicaudatus while feeding on wild figs (1-5) and in G. senegalensis while feeding on a locust (6-10).

10.4 The Use of Nectar and Other Secretions

G. crassicaudatus visited trees as they came into flower and spent periods of up to one hour searching for nectar. The flowering branches were held with one hand and the flowers either smelled or licked. Grabbing movements with one hand were also witnessed, as if the animals were attempting to catch small insects, but they were primarily attracted by the nectar (figure 15b). The male flowers of bananas were visited and a sticky resin obtained by hanging upside-down from the fruiting branch. Leaf buds, leaves and old flowers were also investigated for their exudates.

10.5 The Use of Insects

Both large and small insects were eaten when the opportunity arose but not usually in preference to other foods. No interest was shown towards the numerous moths which were attracted to the fruits damaged by bushbabies while feeding. In Rhodesia, however, G. crassicaudatus regularly caught insects on the lawn in front of a floodlit house. Insects were picked up in one hand in a rather slow grabbing motion and then transferred to the mouth. They were not taken in flight.

10.6 The Licking of Moisture

Although G. crassicaudatus often descended to within a few centimetres of water they were not seen to drink. Bushbabies licked the surface of leaves, sometimes holding them with one hand or biting them off and licking the petioles. This behaviour was uncommon, but it was seen close to a river at dawn when the dew was heavy. Evidently G. crassicaudatus obtain most of their water requirement from their food. This adaptation is carried to an extreme in G. senegalensis which may never drink in the wild or even lick the moisture from leaves (Bearder, 1969).

10.7 Predatory Habits

G. crassicaudatus has been reported to be mainly predatory in its feeding habits, living on birds, eggs, small mammals and reptiles, together with fruit (Hill, 1953; Walker, 1954; Sanderson, 1957; Roberts, 1951). During this study there were many independent and reliable reports of bushbabies killing chickens, doves and other birds and eating only the brain or licking the blood. On the other hand there were equally reliable reports and personal observations to suggest that meat-eating is extremely rare or completely absent in the study populations. During the study, bushbabies were not observed to eat vertebrates of any kind, yet the predatory habits of genets (Genetta tigrina) and marsh mongooses (Atalix paludinosus) were witnessed, despite the fact that these species were seen much less regularly. It is unlikely that predation by G. crassicaudatus would have been missed.

In order to assess the predatory potential of G. crassicaudatus a pair of doves was introduced to four wild-caught bushbabies in a cage approximately four metres square. The doves immediately took over the nest box previously used by the bushbabies and subsequently raised two

clutches without harm. The complete lack of interest in birds as a source of food was confirmed by wild bushbabies which ignored roosting birds at night, even after they had been induced to sing by playback of tape recordings.

The dentition of G. crassicaudatus and their ability to make quiet and stealthy movements indicates that they would be quite capable of catching and killing birds as large as chickens. Likewise, the habit of returning to a regular source of food coincides with reports of chicken houses and dove-cotes being depopulated over a period of several nights. Walker (1969) cites reports of bird-mobbing as evidence of predation on birds by Perodicticus potto, since mobbing is usually limited to predators. This is also known in the case of G. crassicaudatus. These species, however, are rarely encountered during the day and they are approximately the size and shape of a domestic cat, so it may be a case of mistaken identity.

The most plausible explanation for the contrasting impressions concerning predation is that meat-eating is not a universal characteristic of the species but a local habit which may be widespread within one population while being absent from another. If such is the case, it provides an interesting parallel with the lamb-killing and meat-eating habits of baboons (Papio ursinus) which are apparently learnt and transmitted within a population and may spread from one population to another (DeVore and Hall, 1965).

10.8 Discussion of Feeding Habits

The discovery and use of food supplies involves the complex interrelationships between the physical structure of the animal, its special senses, modes of locomotion and method of foraging. Knowledge of the home range and the ability of the animal to memorise the positions of short-term or seasonal food sources may be important. There is even a relationship between food ecology and the social structure of a species (Eisenberg et al., 1972).

The characteristics of locomotion and range movement of G. crassicaudatus are considered in detail elsewhere (sections 11 and 15). It is noted that bushbabies appear to have a thorough knowledge of some food sources within their home ranges. Gum licks in particular provided a fairly regu-

lar supply of food throughout the year. Bushbabies were observed to move rapidly and directly to these spots from distances as far as one hundred metres. When the gum licks had been used repeatedly by several animals, they became unproductive and the lengths of the visits decreased accordingly. Eventually a gum lick was no longer visited for a while and other places were favoured. In this way the bushbabies could usually obtain gum from at least one or two sources at any one time of the year. This was particularly important in the winter when gum formed slowly. During the spring and summer months when gum and other foods were readily available, the bushbabies moved rapidly from one lick to another or they ignored them completely.

Fruit trees, which provided a less regular supply of food, may have been recalled in a similar way, but it is quite likely that they were merely discovered during the normal course of range movements. This type of movement has been described for the prosimians of Gabon by Charles-Dominique (1971). By continuous exploration of the home range, trees which were coming into fruit were found before old fruit supplies had been exhausted.

When moving slowly G. crassicaudatus made searching movements of the head while sniffing which enabled them to find foods such as insects and seeds or occasional small fruits and bits of gum. Although bushbabies have sensitive night vision and good powers of accommodation (Tansley, 1965), there is evidence to suggest that the sense of smell plays an important role in the discovery of food. Trees which bore abundant fruits or flowers had a strong smell which could be detected at a distance by the observer. Bushbabies would go out of their way to reach these trees while they were productive, to the extent of going across the ground, even if they did not visit them at any other time during the year.

An experiment was performed in order to clarify the relationship between the senses and the exploratory movements of G. crassicaudatus. Honey was smeared at various points within the home range of a group in the main study area and renewed at regular intervals. The bushbabies initially discovered the honey during the normal course of movement but they then moved directly to other licks nearby. On the following nights they went to these honey spots without hesitation, while others remained

undiscovered. It therefore appears that small sources of food are not detected from a distance but once they have been found they are remembered.

The foraging techniques of G. crassicaudatus conform closely to those of Perodicticus potto which are also predominantly frugivorous (Charles-Dominique, 1971). On the other hand the senses of vision and hearing seem to be much more important in the feeding habits of predominantly insectivorous species such as G. demidovii and G. senegalensis (Charles-Dominique, 1971; Lowther, 1939). G. crassicaudatus use their hands in a similar way to G. senegalensis, although they lack the stereotyped prey-catching strike (Bishop, 1964). Jolly (1964) notes that both G. crassicaudatus and Perodicticus potto will perform manipulation tasks more readily when the bait can be seen and not merely smelled.

Martin (1972b) points out the importance of considering dentition, particularly the anterior dentition, when discussing dietary adaptations in the lemurs and lorisoids. He suggests that the procumbent arrangement of the lower incisors and canines (to form a tooth-scraper) which is common to both these groups, is primarily an adaptation for scraping and prising in order to obtain plant food such as gum. It has been noted in this study that scraping was not observed during gum-eating in G. crassicaudatus nor was it seen in G. senegalensis (Bearder, 1969). This is surprising if the teeth were originally developed for such a purpose. G. crassicaudatus, however, did use the tooth-scraper for obtaining the pulp from hard-shelled fruits. Other authors, particularly Buettner-Janusch and Andrew (1962), argue that the primary function of the tooth-scraper is that of grooming which is more in keeping with the present observations.

11. LOCOMOTION

Galagos, in common with other primates, have a fundamentally arboreal mode of locomotion aided by the grasping action of the hands and feet. The morphological and behavioural adaptations of recent and fossil prosimians and other primates have been evaluated with clarity by Walker (1967a), Napier and Walker (1967) and Martin (1972b). It emerges from these studies that adaptations for different types of locomotion amongst the Lorisinae and the Galaginae (and equally, amongst the lemurs) have probably been derived from an ancestral pattern rather like that found in the extant Microcebus murinus (Martin 1972b). The ancestral form most likely had a generalized locomotor repertoire showing some degree of hind-limb domination.

The locomotion of G. crassicaudatus in their wild state has not previously been described in any detail. Consequently, assumptions have been made which are not borne out by observations in the field. The above-mentioned authors have classed this species, together with other galagines, indrises, tarsiers and Lepilemur, as specialized vertical-clingers-and-leapers. This is based on morphological criteria such as the intermembral index (the ratio of the length of the humerus and radius to the length of the femur and tibia) and measurement of the proximal tarsal bones. Each of these techniques places G. crassicaudatus within the same category. It will be demonstrated that in fact this species tends towards a generalized quadrupedal form of locomotion more like that of the Cheirogaleinae; most Lemurinae and Daubentonia, despite its morphological specializations. The similarities and differences between the locomotion of G. crassicaudatus and other galagos are noted, with particular reference to G. senegalensis.

11.1 Walking and Running

Slow locomotion in G. crassicaudatus may be described as a 'cat-like' prowling along the tops of branches which increases in speed to a trot or run. The nature of this movement, which was the most common method of progression, is illustrated in figure 17. It is similar to the movement

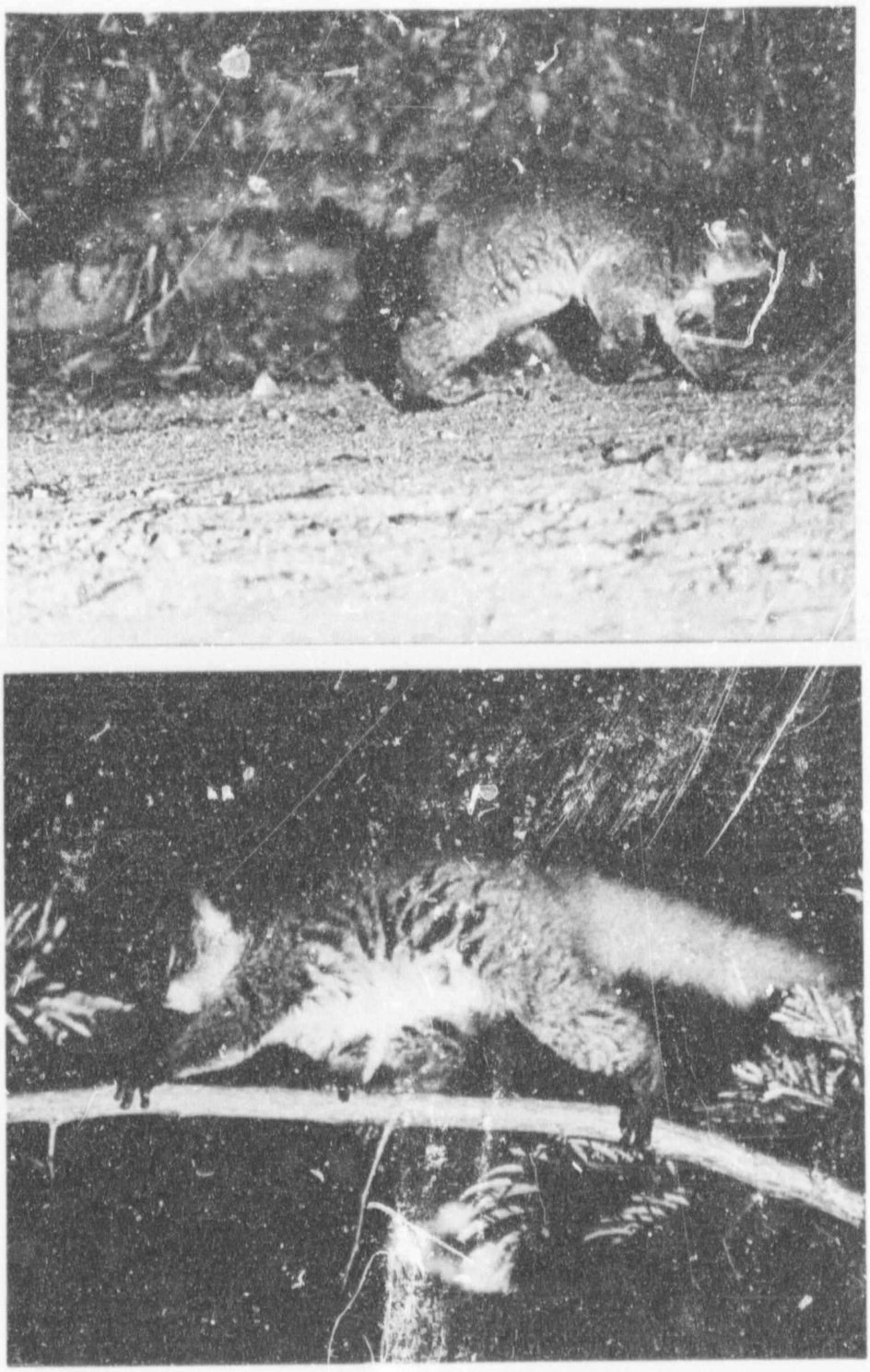


Figure 17. Night photographs of locomotion in G. crassicaudatus. (a) The usual method of progression over open ground. (b) 'Potto-like' walking along a branch.

of Perodicticus potto which, although generally slower, may be as rapid as a feline trot (Anderson, 1971). As in the potto, the body sways from side to side as the hind foot is brought forwards to meet the hand on the same side of the body while the other limbs are fully extended. This fluid movement becomes incomplete as its speed increases and the swaying is less noticeable. When the animals walked or ran on small or roughened branches the hands and feet maintained a firm grip on the support (see Bishop, 1962). On smooth or flat surfaces, however, the hands and feet were splayed open with the pollex and hallux widely spaced from the other digits and the fingers bent upwards at the proximal interphalangeal joints (figure 18). The hands were clenched when they left the support and the foot rotated to bring the weight forwards onto the toes before the next step (figure 19). G. senegalensis has been observed to walk or climb along branches, particularly where they are too small or too dense to allow a jump. It may also run along the top strand of a barbed wire fence for as far as seventy metres. This species, however, does not walk or run on the ground (Bearder, 1969). Basically similar running movements have been described for G. demidovii and Euoticus elegantulus, but they are secondary to jumping (Charles-Dominique, 1971).

11.2 Jumping

Four types of jumps were observed in G. crassicaudatus: quadrupedal hops, short leaps, long leaps and saltation.

11.2.1 Quadrupedal Hops

Hopping involved both the fore and hind limbs in a slow galloping action shown in figure 20. Both hands were moved forwards onto the substrate and the feet brought up to meet them. This action was often interspersed with running, particularly when the animal was moving along large branches. It was also a common method of progression on the ground, a feature shared by Microcebus murinus (Martin, 1972a), but not by G. senegalensis (Bearder, 1969).

11.2.2 Short Leaps

Leaps of up to two metres were made between trees without losing height, providing a good support was available on which to land. The hind limbs provided the propulsive force while the arms took the initial impact of



Figure 18. Photographs illustrating locomotory postures in G. crassicaudatus. (a) Descent through a thorn tree. Note the positions of the fingers. (b) Walking along a branch. Note the position of the hands and feet.

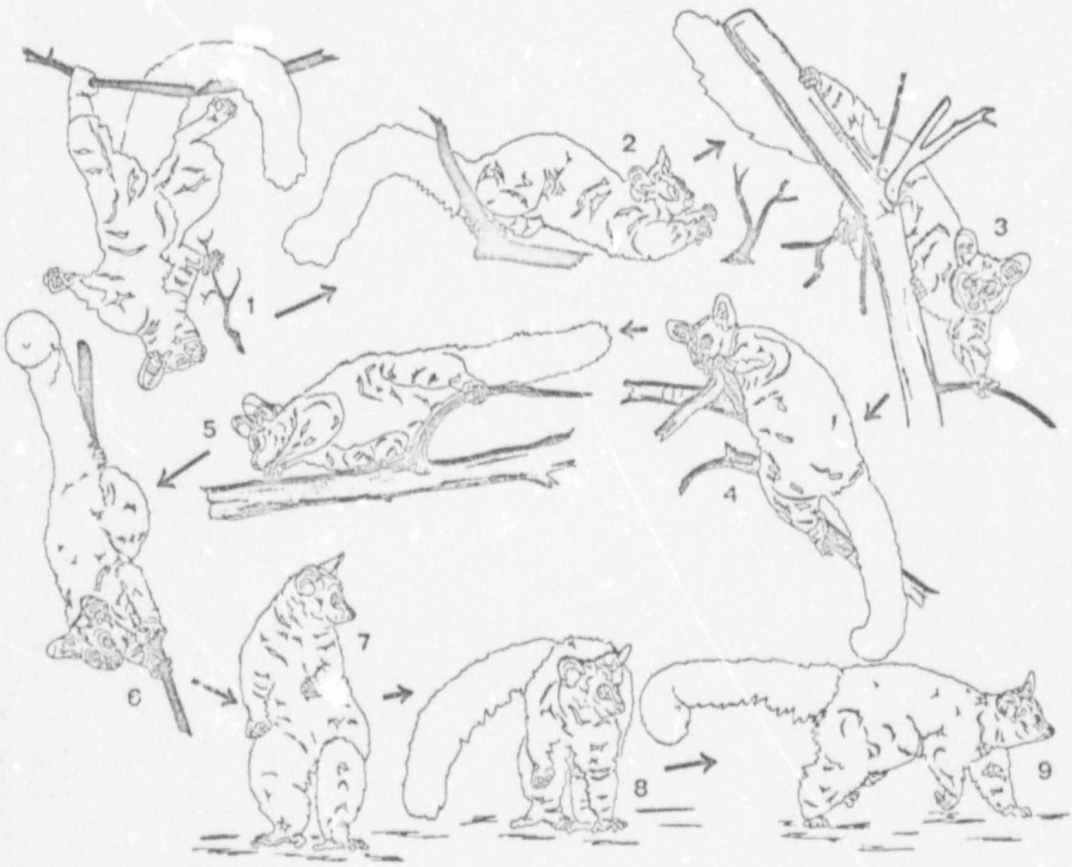


Figure 19. Drawings taken from photographs of G. crassicaudatus to illustrate a typical sequence of movements through the trees and on the ground.

landing (figure 21). Bushbabies were observed to jump horizontally in this way, or obliquely upwards when moving between the trunks of small, closely-spaced trees or when jumping into a tree from the ground. Short jumps of a few centimetres are occasionally performed in this way by G. senegalensis (personal observation, figure 22), but usually the hind limbs are brought forwards on landing. Initial use of the fore limbs on landing has been demonstrated for G. demidovii, G. alleni and Euoticus elegantulus by Charles-Dominique (1971) and it is a characteristic of vertical-clingers-and-leapers.

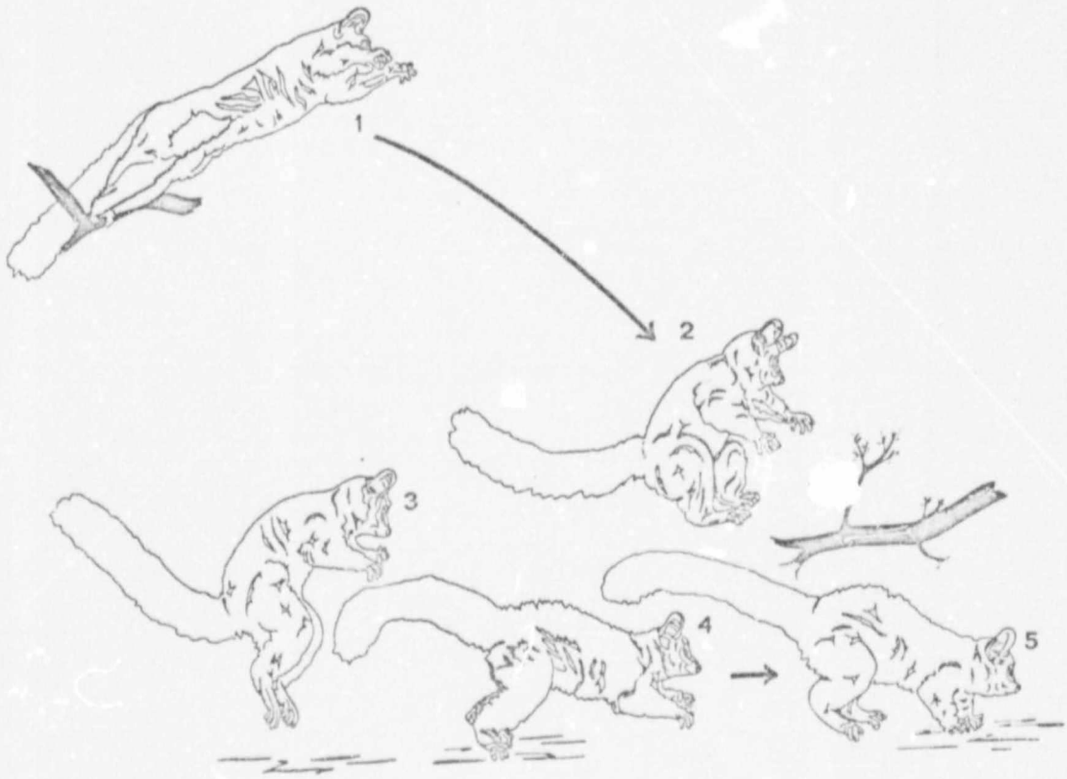


Figure 20. Drawings taken from photographs and field sketches to illustrate some jumping abilities of G. crassicaudatus. (1) The arms are raised sharply on take-off. (2) The arms and legs take almost equal impact on landing. (3) Saltation. (4) Quadrupedal hopping.

G. crassicaudatus did not generally jump between trees if it was able to climb, but it jumped in preference to descending onto the ground. In the absence of an obviously firm support these short jumps were often preceded by side-to-side movements of the head, hesitation and even vocalization. This behaviour was equivalent to that of G. senegalensis before making long leaps or descending onto the ground (Bearder, 1969). In both cases the indecision appears to be related to the animal's vulnerability if it should fall.

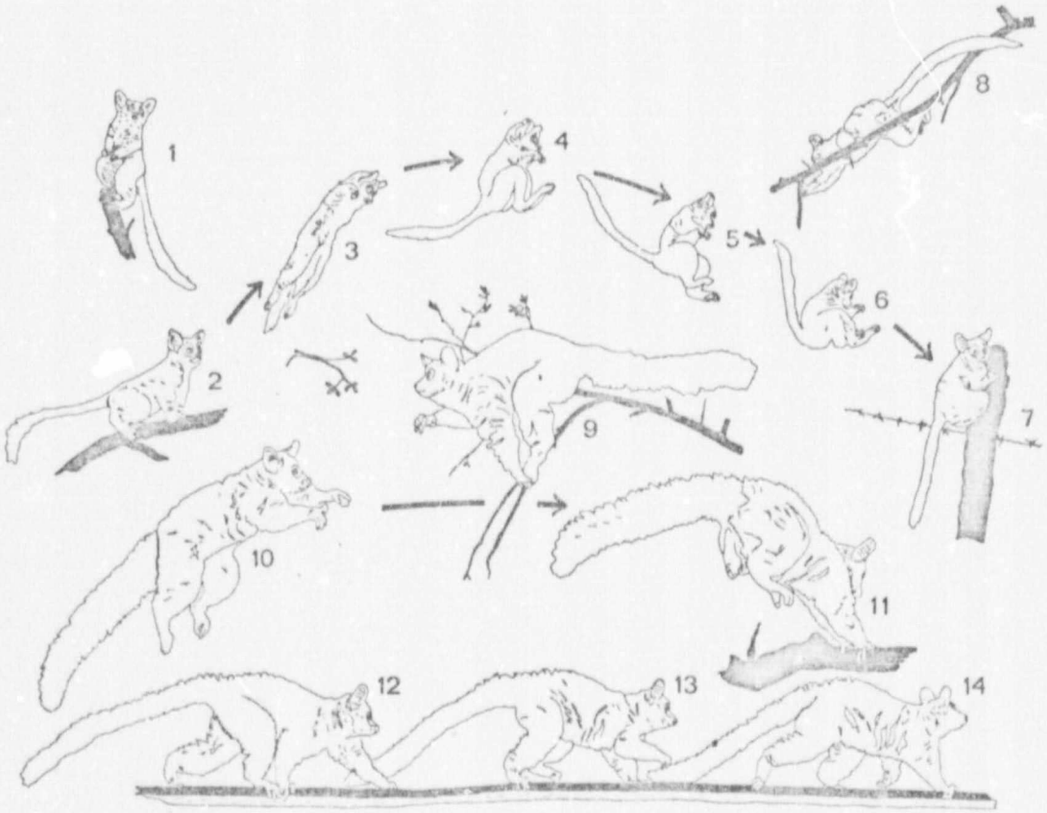


Figure 21. Drawings taken from photographs to show common types of locomotion in G. senegalensis (1-8) and G. crassicaudatus (9-14). Note the difference between the typical short jumps of the two species (2-7 & 10-11).

11.2.3 Long Leaps

G. crassicaudatus occasionally made long downward leaps or drops. While the drop was up to five metres long in a vertical direction the horizontal distance travelled was seldom more than three metres. The hind limbs provided the propulsion and the arms were raised sharply above the head as the animal took off. The hands and feet were then held forwards in such a way that the force of landing was distributed evenly between them. Additional cushioning was provided by the flexibility of the branch on which the animal landed (figure 19). This method of progression between trees has been described for Euoticus elegantulus, with the difference that the lateral extension of the limbs prior to landing is much greater (Charles-Dominique, 1971).

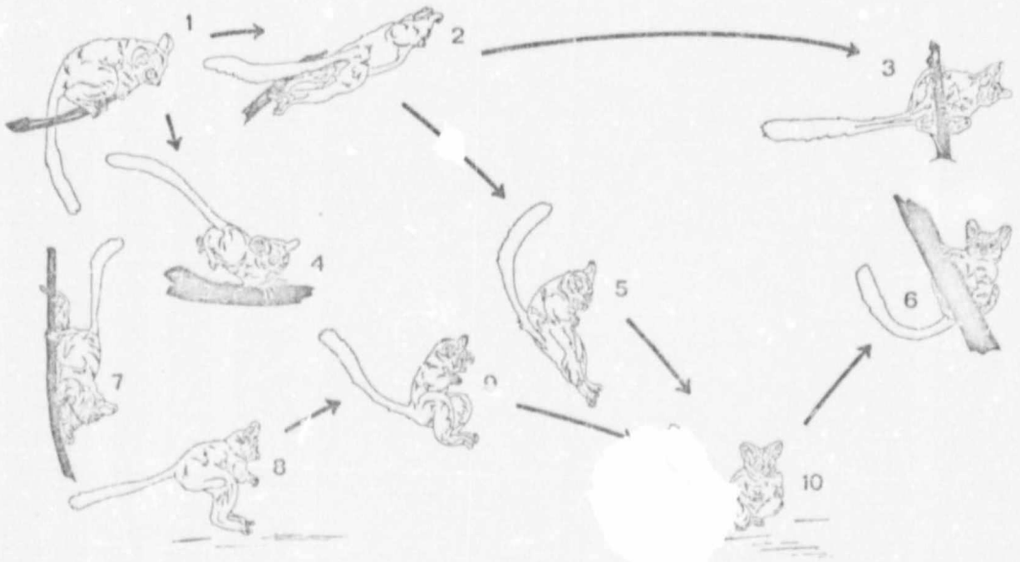


Figure 22. Drawings taken from photographs to illustrate some jumping abilities of G. senegalensis. The arrows indicate possible sequences. (2) The arms are raised sharply only during extremely long jumps (above four metres) (5-10-6) Jumps may be made onto the ground and immediately back into a tree using only the hind limbs. (8-10) Saltation.

The long leaps of G. senegalensis differ with regard to the movements of the hind limbs and tail (figures 21 and 22). Horizontal jumps of nearly five metres can be achieved when the arms are extended forwards on either side of the head (Bearder, 1969) while shorter jumps are made with the arms held against the chest. This is unusual amongst the Galaginae and is related to the fact that G. senegalensis, unlike other galagos, raises the tail sharply and brings the hind limbs forwards to take the initial impact of landing (Hall-Craggs, 1965). The leaping abilities of other bushbabies have been described by Charles-Dominique (1971). The striking feature of G. demidovii, G. alleni and G. senegalensis is that they are adept at jumping vertically from one horizontal support to another by rotating their bodies in mid-air. This ability is lacking in Euoticus elegantulus and G. crassicaudatus.

11.2.4 Saltation

G. crassicaudatus was capable of making kangaroo-like hops on the hind limbs in a way which is illustrated in figure 20. The movements were clumsy and used relatively rarely for progression along the ground. G. senegalensis makes expert use of saltatory leaps when on the ground, figure 22 (Bearder, 1969), but they have not been described for other bushbabies.

11.3 Climbing

The remarkable climbing abilities of G. crassicaudatus have already been mentioned in connection with its feeding habits. In common with other prosimians an excellent grip can be achieved due to the extreme opposability of the digits and the arrangement of friction pads on the palms and soles. These are particularly well developed distally to form swollen pads beneath the nails (Bishop, 1964). G. crassicaudatus adopted a great variety of postures in climbing from place to place (figure 19). They were observed to hang from one or both legs in order to catch hold of a lower branch before dropping down. They often climbed beneath a branch or used spiralling movements to climb from a vertical trunk onto a horizontal limb. The most common method of moving between trees was by deployment of weight across the ends of adjoining branches. The animal usually grabbed the next branch with one hand, or occasionally with both hands, and pulled it nearer before stepping across (figures 19(2) and 23).

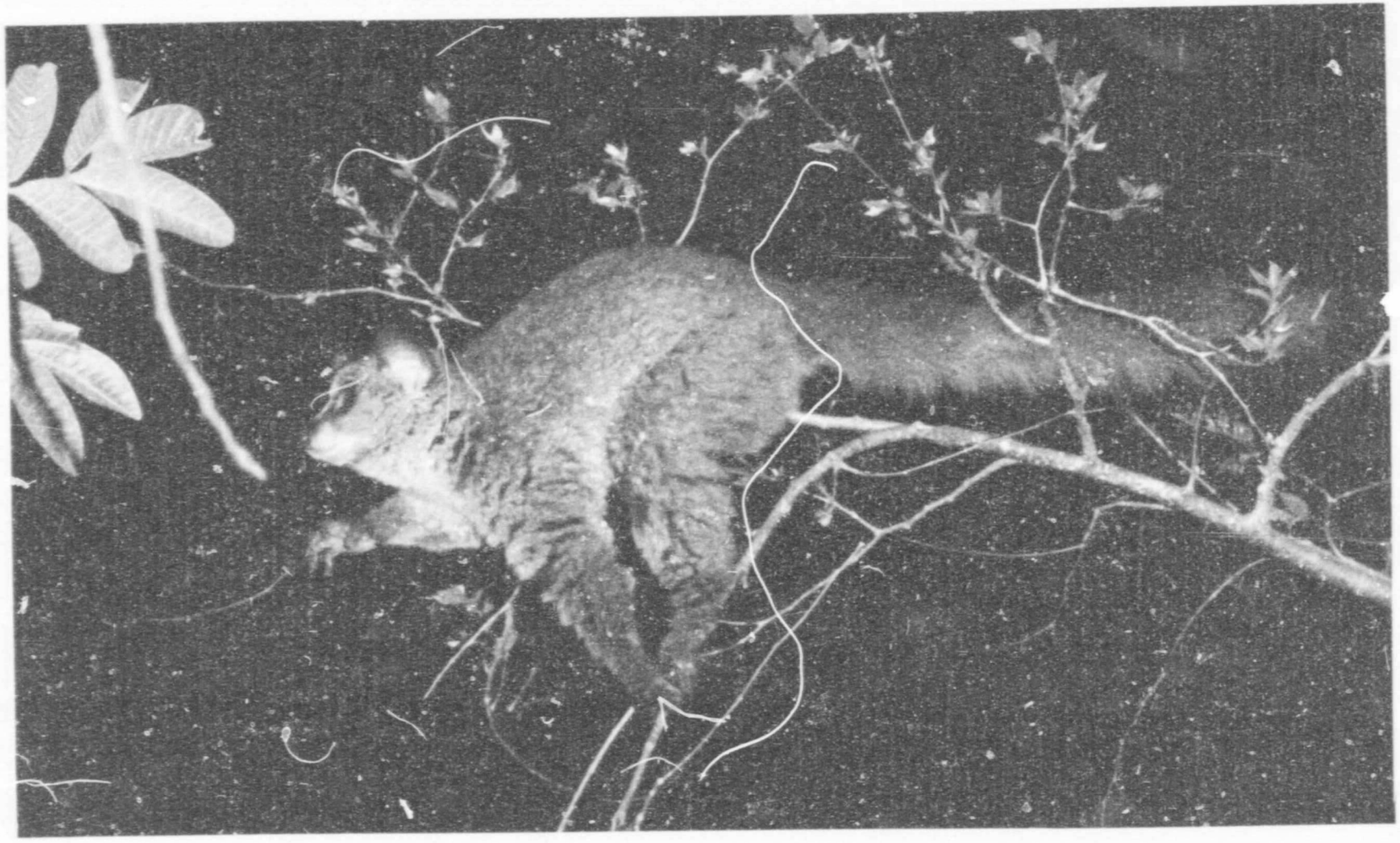


Figure 23. Night photograph of a G. crassicaudatus to show the start of movement between trees without jumping. The animal maintains perfect balance while grabbing for another branch which it pulls nearer and then steps carefully across.

Perfect balance was maintained with the help of the thick tail and the weight transferred slowly and evenly to the new branch before the other was released. G. crassicaudatus also made use of climbers in order to ascend or descend, always moving head-first and frequently reaching across from one climber to the next. Finally, they sometimes employed a looping action in order to descend tree trunks. The body was bent caterpillar-fashion with the legs clasped on either side of the support and the hands gripping the bark.

Many of these actions are more characteristic of the Lorisinae than they are of other members of the Galaginae. Spiralling movements and looping have been described for Perodicticus potto by Walker (1969) and Charles-Dominique (1971) while reaching and climbing carefully between branches is reported for Perodicticus potto (Charles-Dominique, 1971), Loris tardigradus (Rahaman and Parthasarathy, 1970), Nicticebus coucang (Ehrlich, 1969) and Microcebus murinus (Martin, 1972a). The first three species are classed as having a specialized quadrupedal form of locomotion and the latter as having a generalized quadrupedal gait. No equivalent movements are reported for any other species of bushbaby.

11.4 Locomotion on the Ground

Previous records of locomotion in G. crassicaudatus indicate that movement on the ground is achieved by means of saltation (Hill, 1953). On the contrary, observations during the present study show that saltation is rare. Bushbabies were observed on the ground on seventy-five occasions during which saltation was seen eight times (11%, figure 20). Four of these were following the release of bushbabies after they had been trapped and the only instance when more than two or three hops were made at one time occurred during a bout of intra-specific chasing. The obvious reason why saltation has been noticed is that it takes place when the animals are disturbed.

Other behaviours observed during periods spent on the ground are illustrated in figures 17, 19 and 20. They can be represented proportionally as indicated in appendix 8. Walking occurred in 61% of all periods; running in 24%; standing in 23%; quadrupedal hopping in 23% and sitting in 17%. It can be seen that walking was by far the most common mode of locomotion, while running and quadrupedal hopping occurred with roughly equal frequency. G. crassicaudatus did not usually move rapidly across the

ground but proceded cautiously, standing upright now and then to survey the surroundings. In this way they were able to detect any possible danger and respond by moving quickly to the nearest tree. Walking and running were reminiscent of Lemur catta, with the tail held in a characteristic curve (figure 17). They were commonly performed on flat surfaces such as roads, where bushbabies were seen to cover up to 100 metres at a time. Alternatively, in grass and scrub, the animals progressed by means of quadrupedal hops.

11.5 The Locomotion of Lame Animals

In Rhodesia, two bushbabies were discovered which had serious damage to their limbs. In one the left leg was missing below the femur and the wound had healed completely. The second had lost most of the right leg, while its left hand had been crushed and remained unhealed. Both animals were active and moved between trees or along the ground. The one leg was sufficient to enable them to make horizontal and downward jumps similar to those which have been described. The second bushbaby moved awkwardly with a rocking motion by stretching forwards with the one hand and bringing the opposite foot towards it. A third individual was rescued from a jaw-trap after its arms had been amputated immediately below the humerus. Following treatment in captivity this bushbaby was able to jump, walk, run or cling in almost any part of its cage using its hind limbs with the aid of its stumps.

These unusual examples are included to emphasize the importance of generalized patterns of locomotion in G. crassicaudatus. Individuals were able to survive in the wild following severe injuries to their limbs, which would probably be impossible in the case of more specialized forms such as G. senegalensis.

11.6 Discussion of Locomotion

The adaptive advantages and ecological significance of slow and stealthy locomotion in prosimians have been discussed by several authors. Walker (1969) notes that the lorises have one feature in common, a slow and stealthy locomotion, which distinguishes them from the active leaping galagos. He suggests that this type of movement, which is ideally suited not to shake arboreal supports, is related to their mode of obtaining food (Walker, 1969, p. 5):

> It seems most likely that the distinct contract in locomotion between the closely related galagos and the lorises is not one related to major differences in diet but rather to the manner in which the food is caught. Galagos catch and eat insects (and the large G. crassicaudatus E. Geoffroy sometimes eats birds (Hill, 1953)) by speed, with a leaping locomotion adapted to this end. Lorises on the other hand, stalk their prey with stealth, making a final snatch when within range.

A different view is expressed by Ehrlich (1969) partly based on the assumption that G. crassicaudatus are active leaping animals. Ehrlich has shown by means of laboratory tests that slow lorises (Nycticebus coucang) are only relatively slow compared to G. crassicaudatus and that in fact they can respond as rapidly in certain circumstances. She proposes that the type of locomotion of Nycticebus coucang is an adaptation for avoiding predators by moving so slowly as to be virtually invisible. This is due to the fact that the visual cortex of some fast-moving carnivores, such as the domestic cat, responds to moving, but not to stationary, stimuli (Hubel and Wiesel, 1962). Further support of this suggestion is provided by the work of Charles-Dominique (1971) on the potto (Perodicticus potto) and the angwantibo (Arctocebus calabarensis). He adds that many nocturnal arboreal predators are guided by the auditory sense in localizing their prey, which emphasizes the advantages of slow, silent movement as a mechanism for avoiding detection. Charles-Dominique has observed that, in the last resort, lorises will utilize active defense mechanisms against predators while galagos merely flee once detected. He concludes that these adaptations in the lorises have extensively modified their feeding behaviour and diet.

The species G. crassicaudatus provides an interesting test case with which to examine these two hypotheses. To begin with, the contrast between the locomotion of the lorises and galagos is not so distinct as has been supposed. G. crassicaudatus do not obtain their food by means of active leaping, but by quiet and careful movements similar to those of the Lorisinae. In addition they show extensive similarities in their diet, yet they remain capable of moving quickly and noisily and they use rapid escape as their only means of defense. This can be explained, for this species at least, if it is assumed that the type of movement is primarily related to the nature of the food supply and not to the adaptive advantage of avoiding predators. This does not discount the fact that the quiet movements of G. crassicaudatus probably help them to avoid

detection by predators, an advantage which is carried to an extreme in the lorises. Many of the similarities in the locomotory and feeding postures of other species of lorisoids show a relationship to common methods of obtaining food, which in turn reflect similarities in their diets (cf. G. crassicaudatus and Euoticus elegantulus; G. senegalensis and G. demidovii).

If a comparison is made between the structure, methods of locomotion and feeding habits of the slow-moving Perodicticus potto, the extremely agile G. senegalensis and G. crassicaudatus, it can be seen that the structure of G. crassicaudatus is similar to that of G. senegalensis, their type of locomotion lies somewhere between that of the other two species and their feeding habits are like those of Perodicticus potto (table 4). This observation supports the view that the ancestors of G. crassicaudatus obtained their food through speed and agility in a similar way to G. senegalensis but they subsequently underwent a behavioural adaptation towards slower stealthy movement in relation to a more frugivorous diet.

Walker (1970) has examined the fossil remains of lorisoids from the Miocene of East Africa and shown that all the known African prosimians from that period most probably used the leaping form of locomotion. He assumes that the development of stealthy locomotion and associated postcranial changes seen in the lorises are post-Miocene modifications of the more primitive long-limbed, leaping condition. This makes the lorises dependent on true forest conditions, whereas more open country is available to the galagos. Furthermore, according to the fossil record, the lorises originated in Africa and later spread to Asia, in which case the link between Africa and Asia must have been forested at that time. The lack of galagos in Asia is explained by assuming that they were not then adapted to true forest conditions (Walker, 1969). This view is supported by the fact that although G. crassicaudatus now appears to be well adapted to forest habitats, they nevertheless show morphological characteristics which indicate a previous adaptation to more open conditions, where indeed they are still found in some instances.

In conclusion it appears that the generalized locomotor repertoire of G. crassicaudatus is not a direct reflection of the ancestral pattern but a secondary behavioural adaptation away from the typical galagine

Table 4. A comparison of the locomotion and feeding habits of Perodicticus potto (Walker, 1969; Anderson. 1971; Charles-Dominique, 1971 , G. crassicaudatus and G. senegalensis (Bearder, 1969, personal observations).

Species	Primary method(s) of locomotion	Secondary method(s) of locomotion	Locomotion on the ground	Diet and method of obtaining food
Perodicticus potto	Slow, stealthy and quiet, climbing sometimes beneath a branch. Weight transferred evenly forwards.	Occasional running. No leaping.	Walk or run as along a branch. Rapid beelines between trees.	Slow moving or stationary, insects and occasional small vertebrates (10%); fruits (55%) and gums (21%) plus leaves and fungi, obtained by careful climbing.
Galago crassicaudatus	Walking or running. Occasional short jumps or longer 'drops' between trees using hind limbs to provide propulsive force.	Stealthy and quiet climbing, sometimes beneath a branch. Weight transferred evenly forwards.	1. Walk or run as along a branch. 2. Quadrupedal hopping. 3. Bipedal hopping (Saltation).	Slow moving or stationary. Insects and occasional vertebrates - birds (5%) fruits (21%); gums (62%); flower secretions (8%) and seeds (4%) obtained by careful climbing
Galago senegalensis	Rapid jumping or leaping using hind limbs to provide propulsive force.	Stepping movements or climbing along fine branches or in dense vegetation. Running along a strand of barbed wire.	Bipedal hopping (Saltation).	Fast moving, flying or stationary insects (40%) and gums (55%) plus nectar, obtained by rapid jumping and grabbing or clinging.

pattern of vertical-clinging-and-leaping. It is the only example among the prosimians of a behavioural adaptation away from leaping towards a quadrupedal type of locomotion which is not matched by skeletal changes (G. crassicaudatus have an extreme intermembral index). This suggests that it is a comparatively recent development. Evidently the similarities in the locomotion of G. crassicaudatus and Perodicticus potto are not a reflection of a very close relationship between the two, but rather a result of convergent adaptation for obtaining similar types of food in the same way.

12. SLEEPING PLACES

At the end of each night's activity, bushbabies returned to particular sleeping places within their home ranges. Whereas G. senegalensis may be seen on a nest or in a tree fork by looking carefully in each suitable tree (Bearder, 1969), the sleeping places of G. crassicaudatus were almost impossible to find during the day. This species usually remained completely hidden from view and could only be traced if its movements were followed before dawn. Thirty-five sleeping sites were discovered in the three study areas, some examples of which are shown in figure 24 and table 5.

Table 5. Examples of sleeping sites used by G. crassicaudatus

STUDY AREA	SLEEPING SITE	TYPE OF TREE	HEIGHT ABOVE THE GROUND (metres)
N.E. Transvaal	Dense tangle of branches and creepers	Diospyros mespiliformis	9
		Syzyguim cordatum	10
		Ekebergia capensis	10
	Flat leafy nest, sheltered	Rhus chirindensis	6
	Forked branch	Cussonia spicata	9
	Branch of a dense thorn tree	Acacia ataxacantha	5
Zululand	Dense mass of climbers	Species unidentified	8
Rhodesia	Bourganvillia climber	Acacia sieberiana	5
	Tree fork	Pinus sp.	12
	Tree fork	Cedrela toona	9
	Hollow beneath a roof	--	4

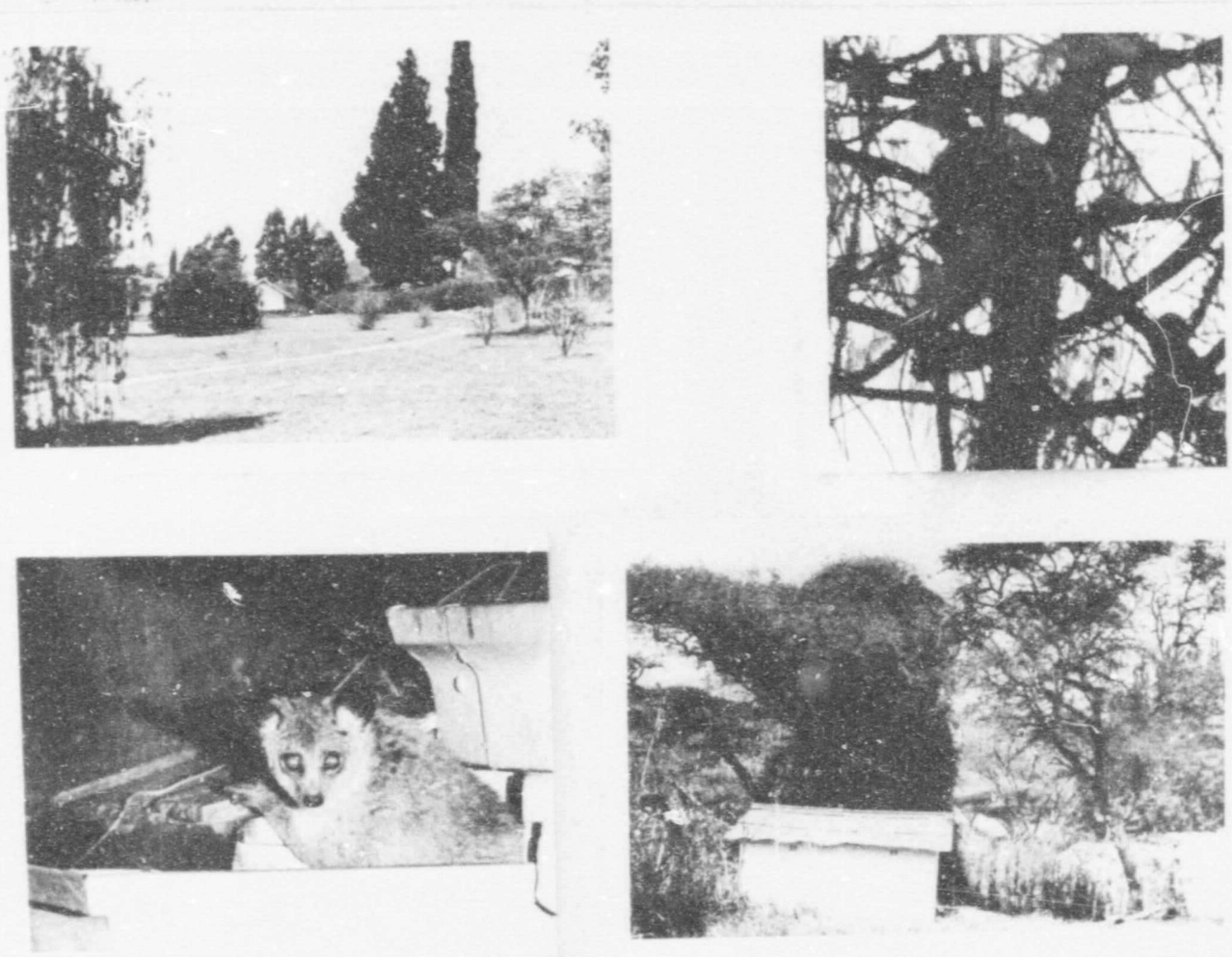


Figure 24. Examples of sleeping places used by G. crassicaudatus. (a) Isolated cypress trees. (b) A high fork in a pine. (c) The space beneath a roof. (d) A dense tangle of bougainvillaea.

G. crassicaudatus usually slept in a dense tangle of branches and creepers at a height of between 5 m and 12 m above the ground. A number of different trees were made suitable by the fact that they supported a dense growth of climbers such as Dalbergia armata and Pteralobium exosum. It is not known whether nests were constructed within these tangles, but on the rare occasions when the animals were exposed from below they could be seen to sleep on the tops of branches or in tree forks, either alone with the tail curled round the body or with others in a huddle. Astley-Maberly (1967) reports that tree hollows may also be used, but this was not observed during the study. In Rhodesia two bushbabies were found occuping a space beneath the roof of a house (table 6).

Table 6. The relative frequency of occurrence of different types of sleeping sites used by G. crassicaudatus (N = 35) in comparison with data for G. senegalensis (Bearder, 1969) (N = 168).

Type of sleeping site	Percentage frequency of occurrence: G. crassicaudatus	G. senegalensis
Branch or fork	91	40
Nest	8	52
Building	1	2
Hollow tree	0	6

Nest-building in G. crassicaudatus appears to be a rare habit, at least in the southern part of its range. Only two nests were found which were used by a single female with small infants. They consisted of inaccessible platforms built at the ends of branches using green leafy twigs and small branches. The mother and her infants slept on top of the platforms which were depressed in the centre and sheltered from above by foliage. Nests have been reported by Jolly (1966a) and Haddow and Ellice (1964) in East Africa where they consist of untidy aggregations of leaves and twigs, often situated in dense foliage or creepers or in the forks of large trees well above the ground.

Fifteen different sleeping sites were found in the home range of one group of bushbabies during the course of a year and their use is examined in detail elsewhere (see section 15.2). With changes in temperature and

and leaf cover particular trees became more, or less, suitable for sleeping purposes and this was reflected by a change in their use. It was not uncommon for more than one sleeping place to be used on consecutive days or by different individuals of the group in a way which has been described for G. senegalensis (Bearder, 1969). The same trees were used by other species for sleeping purposes, presumably due to the fact that they provided excellent cover. Bushbabies were observed to sleep within 2 m of genets (Genetta tigrina), while vervet monkeys (Cercopithecus aethiops) took up residence at night. The present observations on G. crassicaudatus confirm those of Haddow and Ellice (1964) and Jolly (1966a) that particular sleeping trees are used regularly, year after year.

During the day bushbabies are particularly vulnerable to predation by raptorial birds and in Rhodesia they have been reported in the diet of black eagles, Aquila verreauxi (H.D. Jackson, personal communication). It is therefore surprising to find that both G. crassicaudatus and G. senegalensis may occasionally be found exposed to the direct sun (Jolly, 1966a; Bearder, 1969). The adaptive advantage of the use of particular sleeping places may depend on a variety of factors in each species, but some of the advantages are evidently sacrificed at the expense of others. The sleeping places of G. crassicaudatus usually ensured that the animals were well concealed and protected directly from predators, high temperatures or heavy rain and hail. Those of G. senegalensis, although more exposed are usually in thorny trees which provide direct protection from predators (Bearder, 1969). Field observations indicate that G. senegalensis rely on their ability to move rapidly away from danger should they be disturbed during the day and they will change the position of their sleeping places in response to changes in temperature and weather conditions (Bearder, 1969). G. crassicaudatus, on the other hand, relied on concealment and direct protection and this species was not observed to move away from its retreat during the daytime.

The use of open nests cannot be related to any direct protective advantages although they may provide camouflage from below. The timing of nest-building, however, coincides with the onset of the birth season and it can be related to the need to provide a platform for the support of very young infants. Species within the sub-family Lorisinae, in which the infant(s) cling to the mother's fur from birth onwards, have no need for a platform to support the young and they do not build nests. Members

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